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Biological Science Report 8

Evaluation of Insect Defoliation in Baldcypress and Its Relationship to Flooding

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Richard A. Goyer and Jim L. Chambers

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by

Richard A. Goyer
Department of Entomology

and

Jim L. Chambers
School of Forestry, Wildlife, and Fisheries

Louisiana Agricultural Experiment Station
Louisiana State University Agricultural Center
Baton Rouge, LA 70803

Abstract. Global climate change is expected to expose wetland tree species to a multitude of environmental stresses. Sea-level rise will change flood levels and expand the areas subject to flooding because of its effect on backwater flooding and land subsidence. These influences of flooding are the dominant forms of stress in many Gulf of Mexico coastal areas. Presently, freshwater forested areas of southern Louisiana are experiencing a rise in water levels as a result of land subsidence and anthropogenic causes. Successional patterns of baldcypress (*Taxodium distichum* L. Rich.) in particular are being affected by the increased depth and duration of flooding. In recent years, widespread defoliation of baldcypress in Louisiana has occurred in the spring as a result of feeding by the fruittree leafroller (Lepidoptera: Tortricidae; *Archips argyrospila* [Walker]). Defoliation, combined with other stress factors, has affected tree successional patterns in forested wetlands. This project was undertaken to delineate the extent of defoliation of baldcypress and to compare defoliation and refoliation rates under different flooding regimes in naturally occurring field situations.

We compared three hydrologic or flooding regimes: nonflooded, seasonally flooded, and permanently flooded. We also evaluated baldcypress radial growth, short-term basal area increment, dieback of tree canopies, and historical growth and flooding levels.

We found, through aerial and ground surveys, that the fruittree leafroller defoliated baldcypress on 70,000 ha in 1992 and 76,000 ha in 1993. Of this total, approximately 48,600 ha each year sustained sufficient damage so that significant loss of radial and basal area growth resulted when combined with the effects of increased flooding levels and duration. Reduced growth after increased insect defoliation were most severe in permanently flooded areas when compared with regimes that were nonflooded. Of particular ecological concern was the combined effect of insect defoliation and flooding on the health and survival of understory baldcypress saplings. Saplings displayed both canopy dieback and death as a result of repeated defoliation and flooding. With inadequate regeneration already occurring in the baldcypress because of continuous flooding and herbivory, the fruittree leafroller appears to be important in furthering the rapid decline of this species in these ecologically and biologically important wetlands. Further studies, under both natural and controlled conditions, are needed to quantify long-term losses and determine specific mechanisms responsible for resource depletion of these forested wetlands.

Key words: baldcypress, fruittree leafroller, herbivory, flooding, global climate change, Lepidoptera: Tortricidae

The Fruittree Leafroller

The fruittree leafroller (*Archips argyrospila*), a native species, is best known as a pest on fruit trees throughout the northern United States and southern Canada. Although the fruittree leafroller has a wide host range, oaks, apples, and hawthorn are the primary hosts in the northeastern portion of its distribution (Chapman and Lienk 1971). Recently, the fruittree

leafroller has expanded its primary host range to include apricot and citrus in California and baldcypress in Louisiana (Goyer et al. 1995). In Louisiana, the fruittree leafroller primarily infests baldcypress and only rarely oaks. A recent study by Goyer et al. (1995) found three distinct taxa with one feeding on oak and citrus in California, one feeding on oak in Louisiana, and the third restricted to baldcypress in Louisiana. Voucher specimens are placed in the Louisiana State Arthropod Museum, Baton Rouge. In forested wetlands the fruittree leafroller only infests baldcypress (Goyer and Lenhard 1988).

Life Cycle of the Fruittree Leafroller

The fruittree leafroller has one generation per year, with eggs overwintering. In Louisiana, dormant eggs are triggered to hatch by bud break of baldcypress trees during late February and early March. Because of fluctuations of environmental factors and tree phenology, individual eggs within an egg mass or among masses will take 10–16 days or more to hatch. After hatching, caterpillars disperse and seek out the terminal portions of expanding baldcypress foliage, burrow within the cluster of young needles, and begin feeding (inconspicuously). As the foliage expands, the developing fruittree leafroller caterpillars produce silk to roll adjacent needles and branchlets into a tight mass, surrounding themselves individually and then feeding on the foliage inside. However, to meet their food requirements, larger caterpillars usually come out of their "roll" to feed on adjacent foliage. When the caterpillars are disturbed, they move back to their roll or spin down from the foliage by a strand of silk. The silk helps them to escape attack from natural enemies and disperse to new food supplies (Morris and Mott 1963).

Fruittree leafroller caterpillars molt four times (five stages) before pupation (Braun et al. 1990). They change body colors and head capsule width between stages or instars. The first instar larvae are less than 2 mm in length and are cream-colored, while the fifth instars are 2 cm in length and are an apple-green color. The larvae require about 8 to 10 weeks to develop on baldcypress in the field. Eight to 12 days are needed for pupal development. Adults (Fig. 1) emerge between late April and mid-May in Louisiana. They do not feed on trees and are relatively short-lived, surviving only about 14 days. A few days after mating, adult moths deposit egg masses containing an average of 54 eggs per mass on thin twigs of baldcypress (less than 0.7 cm diameter), where the eggs remain dormant until the following spring (Goyer and Lenhard 1988).

Fig. 1. Fruittree leafroller moth and pupal skin on webbed baldcypress foliage.

Damage Caused by the Fruittree Leafroller and Symptoms of Its Presence

The larvae are responsible for ingesting or destroying leaves of baldcypress. Leaves that are not directly consumed are partially injured and, through desiccation, discolor and abscise (Figs. 2 and 3). Through wind-borne and gravitational displacement, most caterpillars are concentrated in the lower portions of baldcypress canopies and often on smaller, understory trees. Thus, severe injury is also concentrated on these trees. When insect populations are high, entire canopies or groups of baldcypress trees (stands) are completely defoliated. Often, baldcypress with "open" leaflet morphology receive more defoliation (Meeker and

Fig. 2. Baldcypress saplings defoliated by fruittree leafroller caterpillars, Iberville Parish, Louisiana.

Fig. 3. Aerial view of baldcypress displaying defoliation symptoms caused by the fruittree leafroller.

Goyer 1993). Repeated defoliation has been observed in several areas of southern Louisiana, with dramatic reductions in radial growth, death of portions of the tree canopy (dieback), and mortality — primarily in the small, understory trees where fruittree leafroller caterpillars concentrate (Fig. 4). Trees that are partially or totally defoliated produce a new crop of needles in June that are generally smaller than those of nondefoliated trees. Repeated leaf loss depletes carbohydrate reserves in the plant; moreover, the new needle crop experiences a shorter growing season in which to contribute to photosynthesis. After repeated, complete defoliation for multiple seasons, reduced growth, dieback, or even mortality can result.

Control of the Fruittree Leafroller

Natural Control

In the wetland environment of Louisiana where the fruittree leafroller is prevalent, there are many organisms that inflict mortality on fruittree leafroller caterpillars, pupae, and adults. Birds, namely prothonotary warblers (*Protonotaria citrea* [Bodaert]) and the Carolina chickadees (*Parus carolinensis* [Audubon]) take larger caterpillars and pupae. The green anole lizard (*Anolis carolinensis* Voigt) also consumes caterpillars on occasion. Most important, however, are other insects. Braun et al. (1990) lists 12 species of parasitic or predaceous insects known to suppress fruittree leafroller populations in Louisiana. Spiders also appear to take large numbers of fruittree leafrollers on a local level. Additionally, two diseases — one caused by a nuclear polyhedrosis virus and the other by a granulosis virus — were first found in 1990 in areas infested since 1983 (Meeker and Goyer 1993).

Despite the variety of natural control organisms, there appears to be only a dampening effect on the area-wide population of fruittree leafroller in southern Louisiana. The absence of egg mortality from natural events is one critical void resulting in high initial survival (Wei 1996). This situation has led to continuous high caterpillar populations. The flooded environment may not be conducive to survival of a large number of beneficial insects needed to regulate fruittree leafroller populations.

Fig. 4. Full-grown fruittree leafroller caterpillars on baldcypress.

Artificial Control

The sensitivity and biological diversity of forested wetlands preclude the use of traditional carbamate or organophosphorus insecticides to control fruittree leafroller populations. Insect growth regulators are also unstable and may have side effects on crawfish and other arthropods.

Tests conducted with *Bacillus thuringiensis* var. *kurstaki*, such as the product FORAY 48B®, demonstrated effective foliage protection with no undesirable side effects on nontarget organisms. This bacterium crystal causes specific mortality to caterpillars only, with no effect on other organisms. Both ground and aerial pilot applications were effective. However, the cost of this form of control could be prohibitive if large areas are to be treated (Goyer 1990). Thus, although an effective spray product is available, economics will limit its use for control to selected, ecologically sensitive, high value areas where fruittree leafroller impacts are deemed to be severe.

Effects of Flooding in Fruittree Leafroller Habitat

Global climate change is expected to expose wetland tree species to a multitude of environmental stresses. Sea-level rise will change flood levels and expand the areas subject to flooding because of its effect on backwater flooding and land subsidence. These effects are the dominant forms of stress in many Gulf of Mexico coastal areas. Construction of flood protection levees, canals, spoil banks, and highway embankments have further altered hydrology in southern Louisiana. Although much attention has been focused on loss of marshes, little has been paid to forested wetlands. Here, the intensity and duration of flooding are important stresses that affect forest composition and growth (Conner and Day 1992). Often, local anthropogenic (e.g., levee construction, channelization, petroleum exploration activities, etc.) changes interact with biological and climatological factors to cause variable levels of stress to the forests inhabiting these areas. Even baldcypress, a flood-tolerant species, is affected by flooding with stagnant waters (Shanklin and Kozlowski 1985; Pezeshki and Chambers 1985a, b). Currently, increased inundation of Louisiana coastal wetland areas is occurring as a result of eustatic sea-level rise and land subsidence (Hoffman et al. 1983; Baumann et al. 1984). Freshwater forested areas in coastal regions of Louisiana also are experiencing a rise in water levels (Salinus et al. 1986; Conner and Day 1988; Conner and Brody 1989). Conner and Day (1992) predict declines in baldcypress basal area (density) and contend that no new seedlings will enter the understory over time as flooding increases.

In recent years, widespread defoliation of baldcypress in Louisiana has occurred in the spring as a result of feeding by the fruittree leafroller (Goyer and Lenhard 1988; Braun et al. 1990; Meeker and Goyer 1993). The fruittree leafroller feeds on both large and small trees and thus is an additional stressor affecting tree successional patterns in forest wetlands.

Objectives

This project was undertaken to accomplish the following objectives:

1. Delineate the extent of defoliation of baldcypress by the fruittree leafroller in south Louisiana and broadly categorize the levels of defoliation within the affected area.
2. Compare defoliation on mature trees to that on immature baldcypress.
3. Contrast defoliation levels and refoliation rates under different flooding regimes (i.e., permanently flooded, seasonally flooded, and nonflooded).

Procedures

Study Areas

To assess the extent of defoliation by the fruittree leafroller to baldcypress, we conducted aerial and ground surveys over the vast area of forested wetlands east of the Atchafalaya River, south to the limits of baldcypress, and eastward to New Orleans.

Within this broad land area, we chose specific study areas in close proximity to a U.S. Army Corps of Engineers (USACE) water monitoring gauge to evaluate differing hydrologic regimes and the interaction(s) with fruittree leafroller defoliation and impact.

As noted in Fig. 5, the three common hydrological regimes in forested wetlands in south Louisiana involve a series of levees, artificial or natural areas that receive run-off flooding, and areas impounded by artificial alterations to water movement. An area in the vicinity of Bayou Chevreuil along the borders of St.

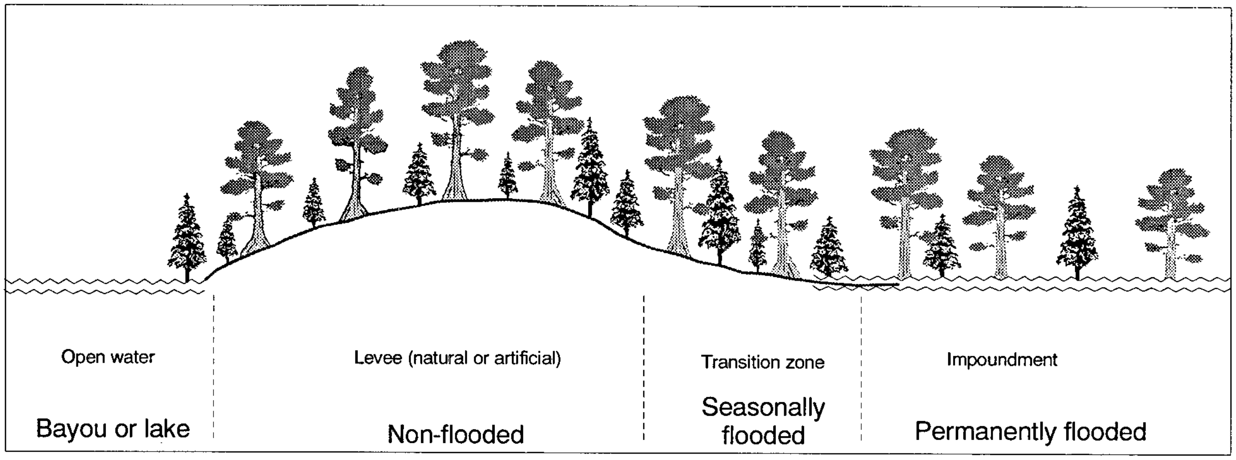


Fig. 5. Hydrological regimes of baldcypress swamps.

James and Lafourche parishes was chosen because it features these three common types of hydrologic conditions. This area was selected also because impacts of flooding on plant and tree composition and growth have been previously studied there (Conner and Day 1992).

Determining Extent of Defoliation

Aerial surveys to detect defoliation caused by the fruittree leafroller have been conducted annually as part of an ongoing evaluation of this insect pest (Goyer unpublished data). Thus, some historical evidence is available with which to evaluate the extent of fruittree leafroller-caused defoliation of baldcypress. During the peak period of caterpillar feeding in late spring (May), two observers and one plotter observed defoliation patterns from a Cessna 172 at an altitude of 457-610 m. Zones of defoliation were sketched onto topographic maps for the 1992 and 1993 seasons following the methods of Knight and Heikkenen (1980). After areas were delineated on topographic maps, several areas were ground-truthed to confirm defoliation by the fruittree leafroller (as opposed to human-caused or other natural phenomena). Areas demonstrating crown discoloration or needle consumption were then compared to determine direction of spread, intensity (degree) of defoliation, and overall occurrence (scattered, area-wide-partial, or complete defoliation).

Determining Defoliation in Relationship to Flooding Regimes

Within the Bayou Chevreuil watershed, we chose three nonflooded, three seasonally flooded, and three impounded (permanently flooded) areas for a total of nine sites. The sites in each of the nonflooded areas (Fig. 6) were on natural or constructed levees adjacent to the present bayou course. These were generally narrow strips 30–50 m wide. We chose flatlands not noticeably impounded near the main bayou course as seasonally flooded study areas and impoundments created by dredging as stagnated, permanently flooded areas. Three transects per regime were established parallel to the bayou to minimize any microsite changes in water depths. We selected 10 trees at two-chain intervals (approximately 40 m) along each transect to evaluate for degree of defoliation during the time of peak herbivore activity (May) in both 1992 and 1993. Each tree within each transect was re-evaluated two or three times after insect defoliation to determine the time interval and extent of refoliation (as a % of live crown with needles). Defoliation was estimated ocularly in 20%± increments and placed into (1 of 5) classes.

At the apparent high and low points along each transect, as determined by sight, meter sticks were tacked to nearby trees to measure water depth and its variation over time. At each visit to that transect, each meter stick was read and water depth (or lack

Nonflooded site.

Seasonally flooded site.

Fig. 6. Example of nonflooded, seasonally flooded, and permanently flooded study areas near Bayou Chevreuil, Louisiana.

Permanently flooded site.

Fig. 6. *Continued.*

of water) recorded. These data then were correlated with data from the USACE (see section on data analyses).

Additionally, we measured the radial growth of trees with a Karlberg microdendrometer, using standard procedures (Bormann and Kozlowski 1962). Two separate measurements at 0.5 m above trunk butt swell were taken at 90° angles to account for individual growth pattern variation of each tree. Measurements were made each June (coinciding with the timing of maximum defoliation) to obtain the annual radial increment. Cores were taken and the average of two cores per tree used to determine age and 5- and 10-year radial growth increments. Cross-dating techniques were used to avoid errors associated with missing or discontinuous rings.

Observational data from our ongoing evaluations have indicated that small, often suppressed or stressed trees are differentially affected by fruittree leafroller defoliation. Thus, we chose 20 small trees (less than 10-cm diameter) to evaluate in 1992 and 1993. These trees all displayed some degree of dieback when first examined and were split evenly (10 each) between seasonally and permanently flooded areas near study transects.

Data Analyses

Water level measurements taken from our two measuring sticks at each seasonally or permanently flooded transect were compared by linear regression analyses with gauge data from the nearby USACE gauge data (use of the gauge was unexpectedly discontinued in the fall of 1992).

Radial increments from both growth cores (average of 2) and the microdendrometer readings were compared for each treatment (hydrologic regime) using analysis of variance. Significant effects were further separated by Scheffe post hoc tests. Furthermore, we conducted Pearson Product Moment correlation analyses of fruittree leafroller defoliation and 1-, 5-, and 10-year tree growth. The statistical package "Data Desk" was used for all statistical comparisons, which are presented in Appendixes A-H.

Results and Discussion

Extent of Defoliation

Extensive defoliation of baldcypress by the fruittree leafroller has occurred each spring since 1983. The area affected has expanded increasingly since that time, and, at present, portions of 14 parishes from the Atchafalaya River east to New Orleans (vicinity) are affected (Fig. 7). In both 1992 and 1993, approximately 60,000 ha received significant (greater than 50%) defoliation. Additional defoliation occurred on a localized basis on small or "edge" trees. The presence of fruittree leafroller webs, without obvious defoliation, was detected in scattered "upland" settings and urban areas where baldcypress grows as a shade tree and an ornamental.

Where baldcypress makes up a major share of the stand basal area (density), the likelihood of increased insect population growth is higher due to food/habitat availability. Thus, in these areas, the effects of defoliation are more readily visible. In 1992, the areas containing stands defoliated most visibly by the fruittree leafroller were (1) an area within the Atchafalaya Basin levee system southwest of Bayou Pigeon to Belle River and westward to Duck Lake; (2) scattered stands bordering Palourde and Verret lakes, and swamplands eastward toward Thibodaux; and (3) a severely affected area surrounding Lac des Allemands and Lake Boeuf east of Thibodaux. By 1992, defoliation had spread northeasterly into the northern portions of St. James and St. Charles parishes. The spread to the southeast in St. Charles Parish was slowed by natural barriers of nonforested wetlands. A pathogenic virus specific to caterpillars was observed to reduce fruittree leafroller populations in portions of the Atchafalaya Basin but was not evident in other areas (Wei 1996).

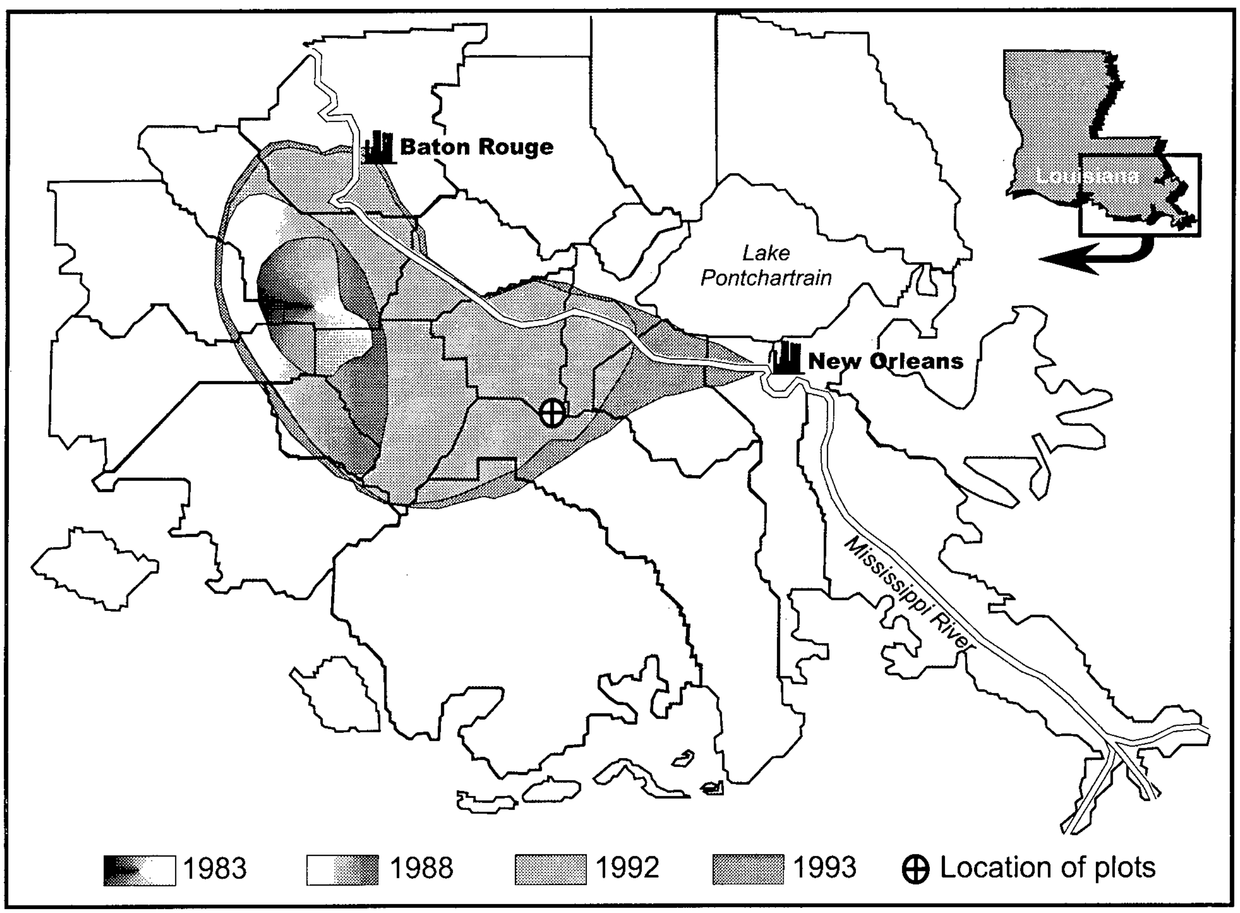


Fig. 7. History of fruittree leafroller defoliation of baldcypress in Louisiana.

In 1993, further easterly shifts in baldcypress defoliation were detected. Aerial flights and several followup ground surveys revealed that the fruittree leafroller had defoliated a large area on both sides of the Mississippi River as far east as Kenner (primarily St. Charles Parish) (Fig. 7). Here, trees have been subjected to several environmental and anthropogenic stresses. The addition of high levels of fruittree leafroller defoliation on a repeated basis may result in dramatic declines in baldcypress vigor in this area. The Pontchartrain Basin is thus likely to have fruittree leafroller defoliation added to the list of future threats, as this insect appears to be spreading farther into that region of Louisiana.

Defoliation of Mature Versus Immature Baldcypress

As noted earlier, small, often suppressed or young trees are more frequently and severely defoliated by the fruittree leafroller. Our project cannot properly evaluate long-term trends in tree health, but short-term effects on small trees (less than 10 cm diameter) were evaluated in both 1992 and 1993. Of the 20 trees studied, 10 were located in a seasonally flooded area, and 10 were in a permanently flooded area near other transects. The crown condition of these 20 trees is described in Table 1. It is important to note that many of these trees are suppressed by a 60-to-75-year-old overstory of baldcypress and tupelo. These 20 trees had most likely been defoliated for 2-3 years prior to the initial exam in 1992 (based on historical evidence of earlier aerial and ground surveys).

The impact of fruittree leafroller defoliation is evidenced by partial to severe dieback of recently live branches in the canopies of these 20 trees (Table 1). Epicormic branching, a physiological response to severe stress or increased solar exposure, was clearly evident on several trees. Often, these short "suckers" make up the majority of the photosynthate-producing leaves present at the time of examination.

It appears from these limited evaluations, coupled with 10 years of related observations, that small baldcypress do not recover fully from complete and often repeated defoliation by the fruittree leafroller. Larger trees refoliate more completely. Of ancillary interest, we noticed a low proportion (about 5–8%) of small baldcypress stems that had recently died (Fig. 8). The causes of mortality were not clearly determined but could easily be interpreted to have been at least partially due to the combined effects of flooding, suppression, and fruittree leafroller defoliation. Observations of similar saplings occurring outside the range of fruittree leafroller impact revealed less than 5-8% mortality.

Table 1. Comparison of annual dieback (%) on understory baldcypress saplings less than 10 cm diameter for two flooding regimes at Bayou Chevreuil, Louisiana, 1992-93.

Tree Number	1992 Dieback	1993 Dieback	Change in Dieback
Seasonally flooded			
1	33	33	0
2	15	25	10
3	50	65	15
4	30	30	0
5	75	67	-8
6	80	90	10
7	10	20	10
8	20	33	13
9	60	60	0
10	90	90	0
Mean	46.3	51.3	5.0[b]
Permanently flooded			
11	20	60	40
12	20	50	30
13	15	30	15
14	15	25	10
15	0	25	25
16	5	8	3[b]
17	17	[a]	[a]
18	40	40	0
19	25	10	-15
20	0	10	10
Mean	15.7	28.7	13.1[c]
Overall Mean	31.0	39.9	8.9[d]

[a]Tree missing (1993).
[b]Change not significantly different by paired t-test $P > 0.05$.
[c]Annual change significantly different, $P < 0.05$ by t-test ($t=2.35$, 8 d.f.).
[d]Overall change significantly different, $P < 0.05$ by t-test ($t=2.96$, 18 d.f.).

Defoliation in Relation to Flooding Regimes

Based on several years of observations, we assert that the fruittree leafroller is truly a wetlands pest in Louisiana. As noted earlier, the occurrence

of serious levels of baldcypress defoliation are closely linked with seasonal or permanent flooding. The continued easterly spread of severe defoliation into the suburban New Orleans area will create an opportunity to further analyze this herbivore's relationship to flooding. In a few cases in 1993, we examined residential areas that were recently created in lowlands where baldcypress predominates. These "islands" received dramatic defoliation as a result of the surrounding high fruittree leafroller population. This project was not designed, however, nor was it of sufficient duration, to clearly determine the suburban

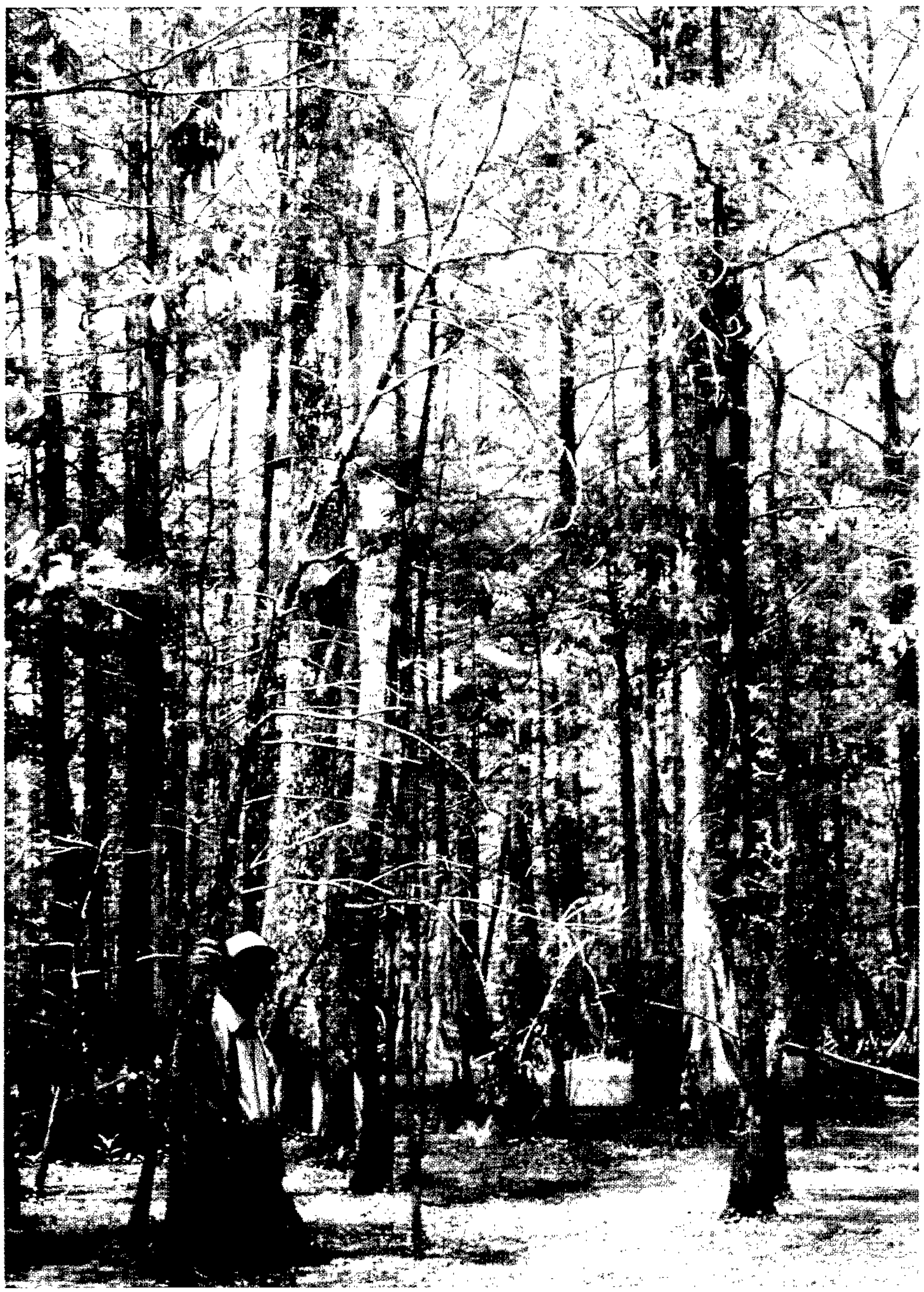


Fig. 8. Understory baldcypress sapling killed by the combined effects of repeated leafroller defoliation and permanent flooding.

problems associated with this phenomenon. Further evaluations are necessary to ascertain the impact of fruittree leafroller defoliation in the suburbs-wetlands interface.

Six-Year Flood Regimes of Study Transects

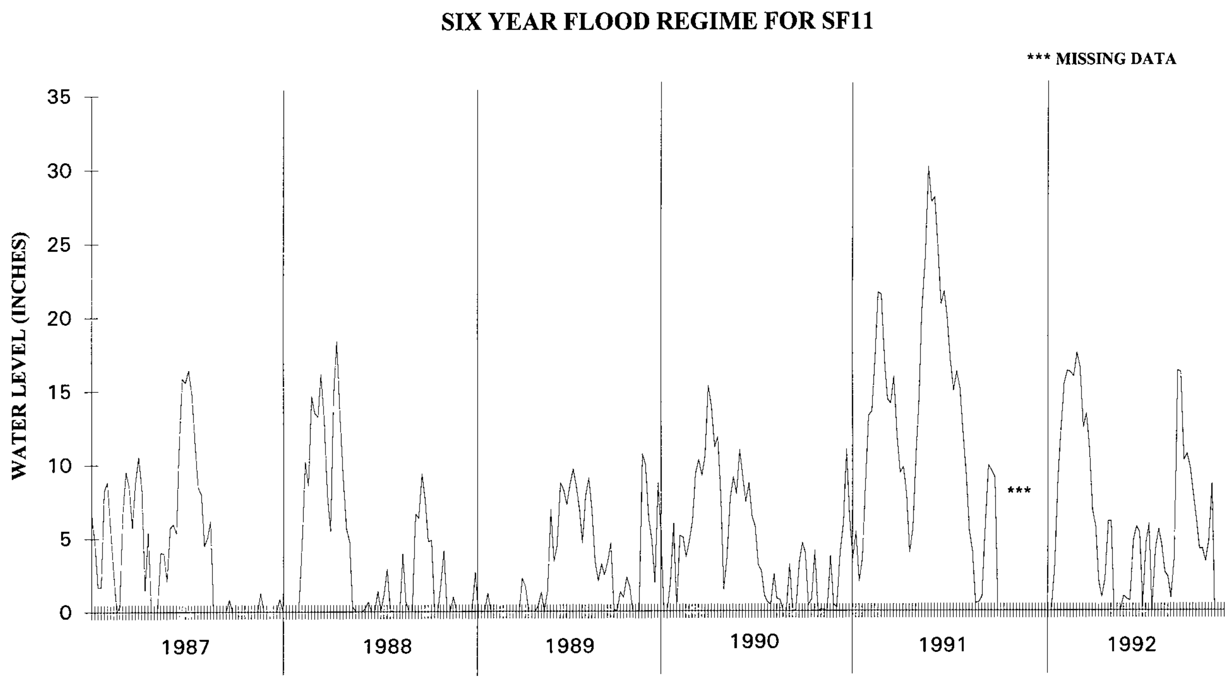
We evaluated the relationship of fruittree leafroller damage and flooding at nine transects near Bayou Chevreuil. Road construction in 1931 and subsequent dredging and levee construction since 1956 have produced major changes in drainage and water levels in the Bayou Chevreuil area (Conner and Day 1992). Other effects on water levels were brought about by breaks created in 1977 in the artificial levees along the bayou. To quantify recent water level histories, estimated past water levels in the selected study areas were depicted from USACE water gauge readings in a manner similar to that suggested by Conner and Day (1988). Floodwater levels shown in Fig. 9 illustrate reconstructed historical trends at two locations along each study transect for the period from 1987 to 1992, using regressions developed from six flooded transects (Table 2).

Water levels in seasonally flooded transects varied widely throughout the year. Higher water levels tended to occur in the winter and spring and lower levels or "dry spells" most often occurred during the summer and fall, along with normal periods of higher evapotranspiration. Considerable variation in the seasonal flood regime is obvious when contrasting water levels on the high microsites, sample points SF11 and SF22, with water levels on lower microsites, sample points SF12 and SF21 (Fig. 9). This pattern indicates that the period of inundation and possible impacts on growth and defoliation may vary dramatically for various microsite locations with the broad definition of "seasonally flooded" conditions. The 1991 flood regimes tended to illustrate higher than normal water levels for the chosen sample plots. This occurrence may relate to the increased incidence of fruittree leafroller defoliation on seasonally flooded transects in 1992, as sudden changes in hydrology or water levels may lead to physiological changes in trees that favor population increases in insect herbivores.

Water level trends on plots originally chosen as permanently flooded also indicate the large variation in floodwater regime between high and low microsites along the study transects. High microsite conditions, as illustrated in transect locations PF11 and PF21 (Fig. 9), actually experienced several periods of little or no standing water, although the soils remained saturated at the surface. Low microsite locations along the transects, such as PF12 and PF22 (Fig. 9) experienced nearly permanent flooding. All microsite conditions along transect PF31–PF32 (Fig. 9) were permanently flooded, although mean water depth varied from approximately 15 to 58 cm along the transect. Sites PF31 and PF32 were located 100 m away from a dredged canal approximately 1500 m from the main Bayou Chevreuil course. Water levels here were less subject to seasonal flow from distant run-off.

Effects of Herbivory and Flooding on Radial Growth

The diameters showing radial growth in ages 1-year, 5-year, and 10-year of baldcypress trees in sample transects (Table 3) reflect the influence of permanent flooding (as compared to seasonal and nonflooded conditions). It is clear that radial growth in baldcypress responds negatively to increased flooding duration under the conditions present at Bayou Chevreuil (Table 4; Fig. 10). These data reflect the combined influences of flooding plus the impact of leafroller defoliation especially during the last 2–5 years. Before then, the leafroller was not present in the study area. Both 5- and 10-year radial growth rates differed significantly at $P < 0.05$ between permanently flooded and nonflooded areas (Table 4). Other comparisons were not significantly different. Dicke and Toliver (1990) and Conner and Day (1992) report similar growth responses to flooding results, although the leafroller was not considered separately in their study. The 1-year radial growth increments measured by microdendrometer also did not differ significantly among transects (Table 3). Although the trees in the permanently flooded area were approximately 10 years younger than nonflooded trees (Table 3), the overall radial growth was so slow as to not affect the comparisons. Thus, when we compared changes in cross surface area (basal area) (Table 5), the permanently flooded transects again added significantly less volume and surface area in the 1992–93 season than did their nonflooded counterparts. Additionally, there was a significant correlation between the 1992–93 growth (radial as well as surface area) and leafroller defoliation ratings at $P < 0.05$.



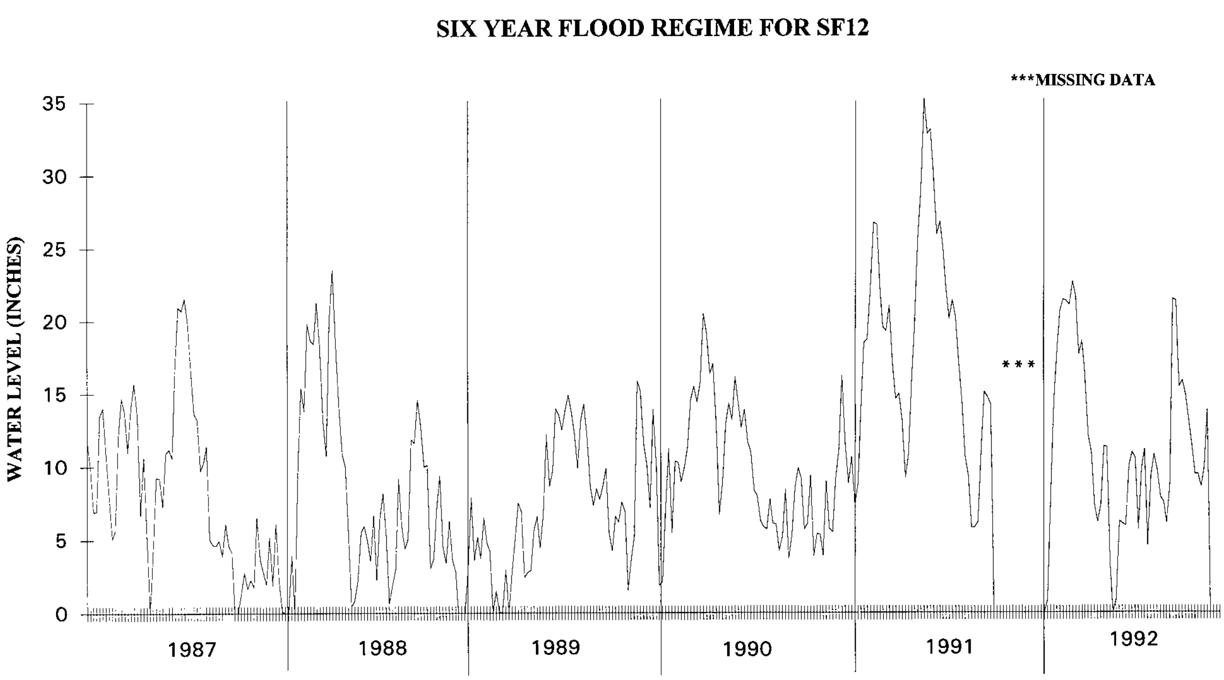
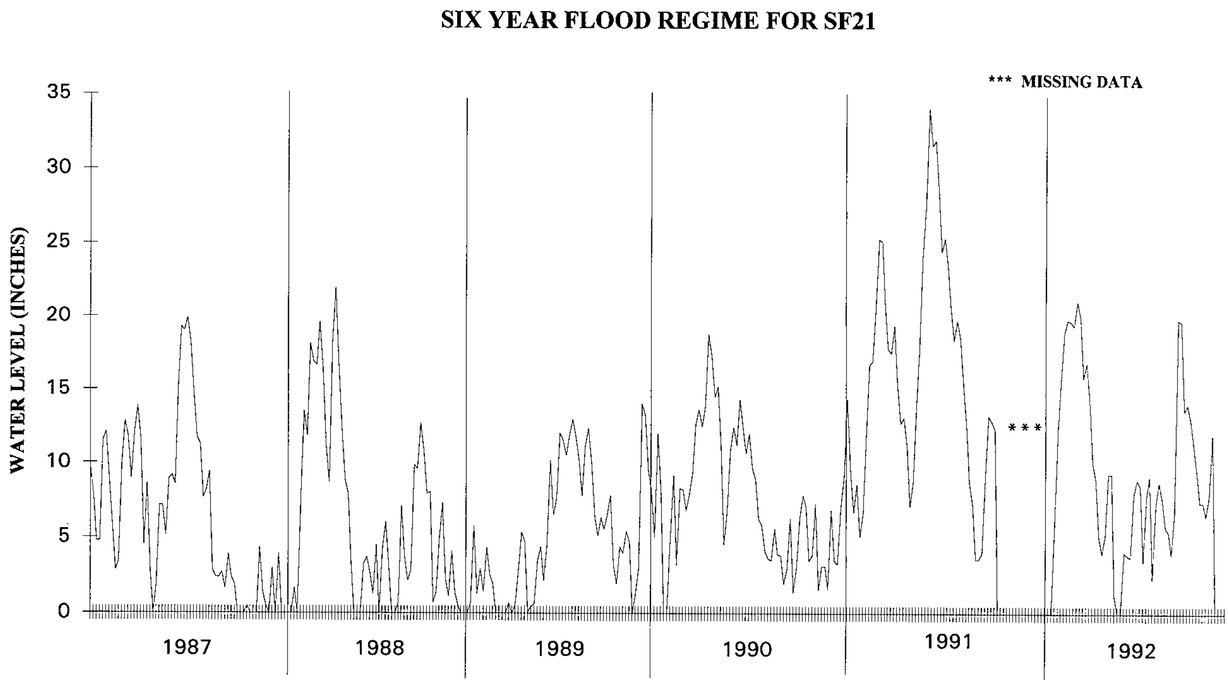
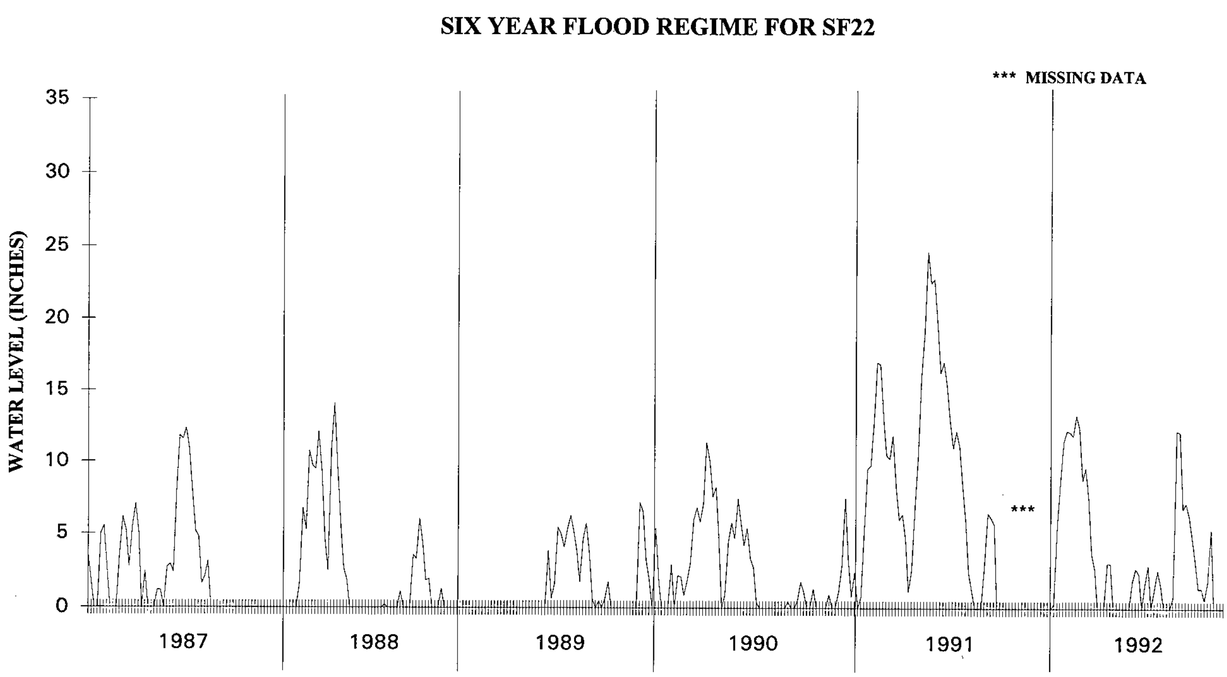


Fig. 9. Six-year flood regime for transects that are seasonally flooded (SF) or permanently flooded (PF) at study sites near Bayou Chevreuil, Louisiana.





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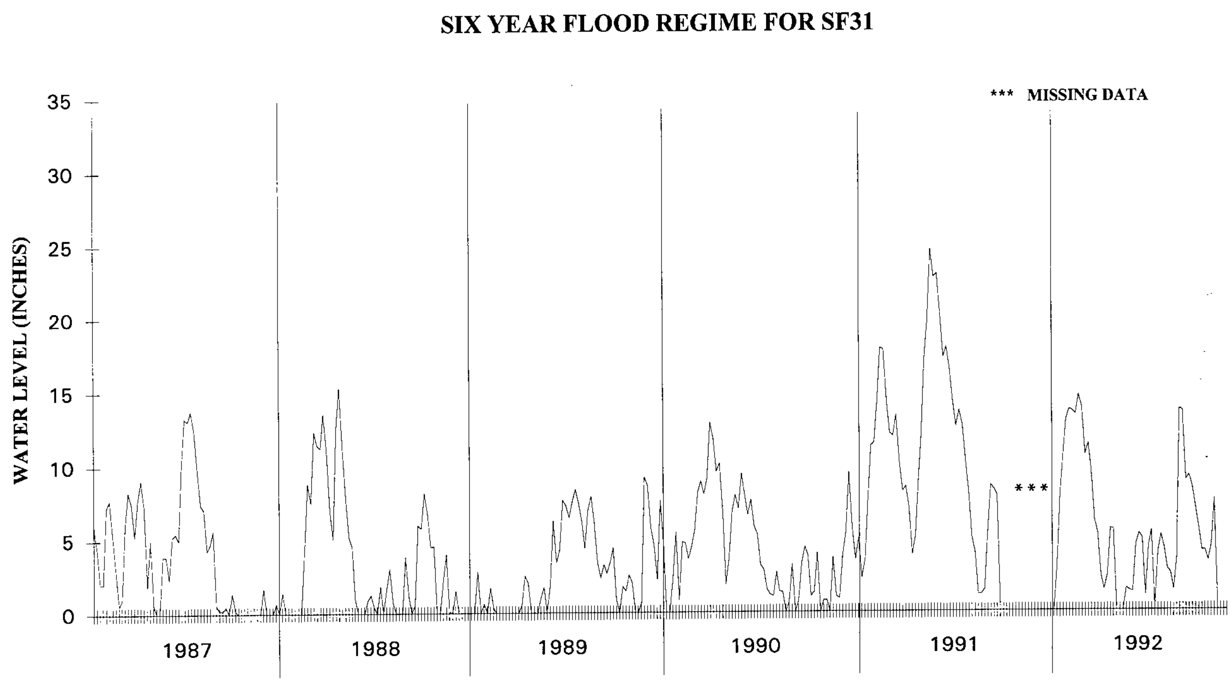


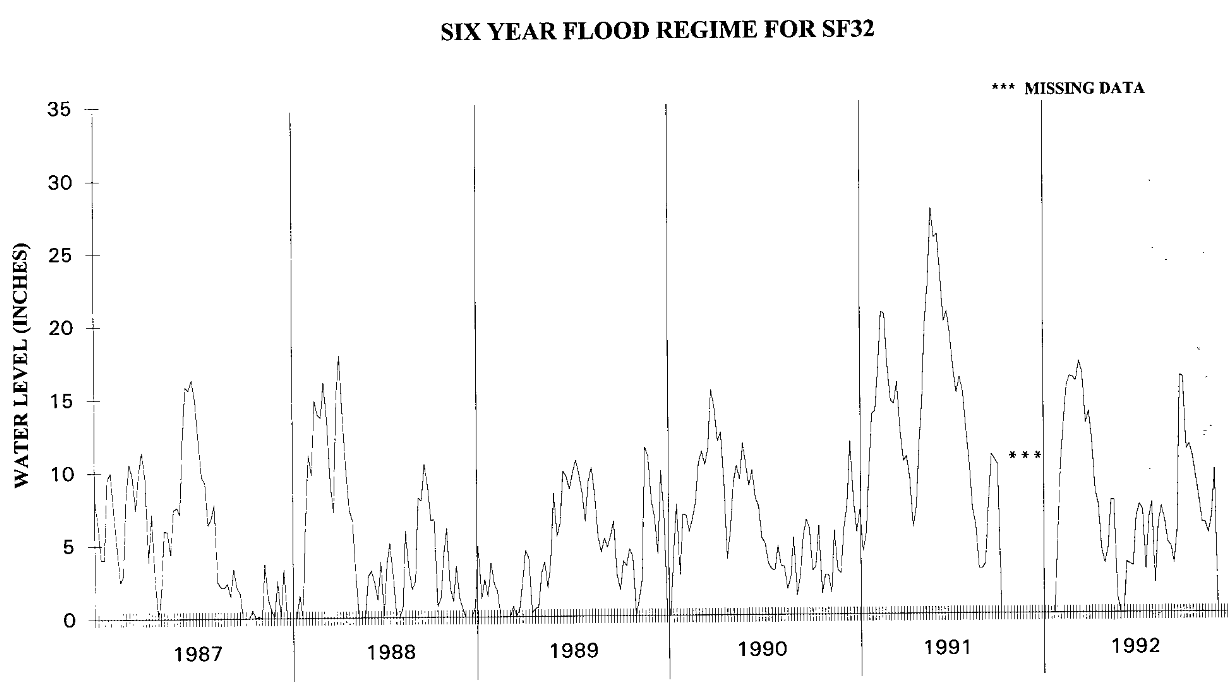
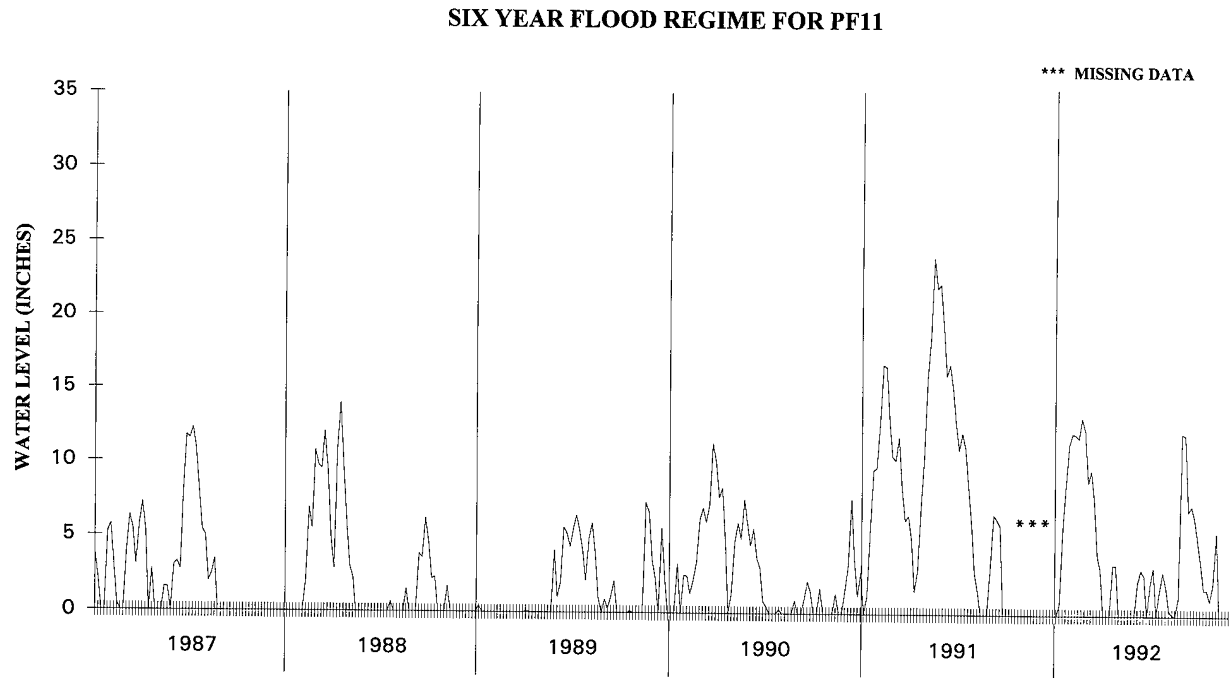
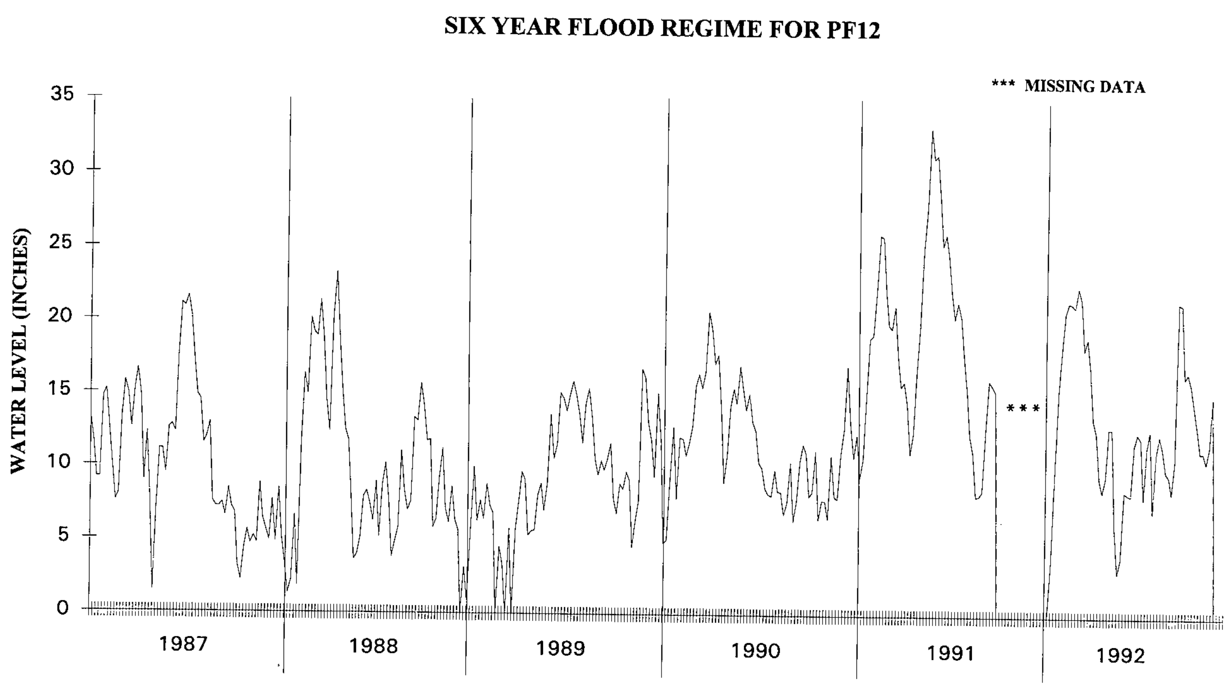


Fig. 9. *Continued.*





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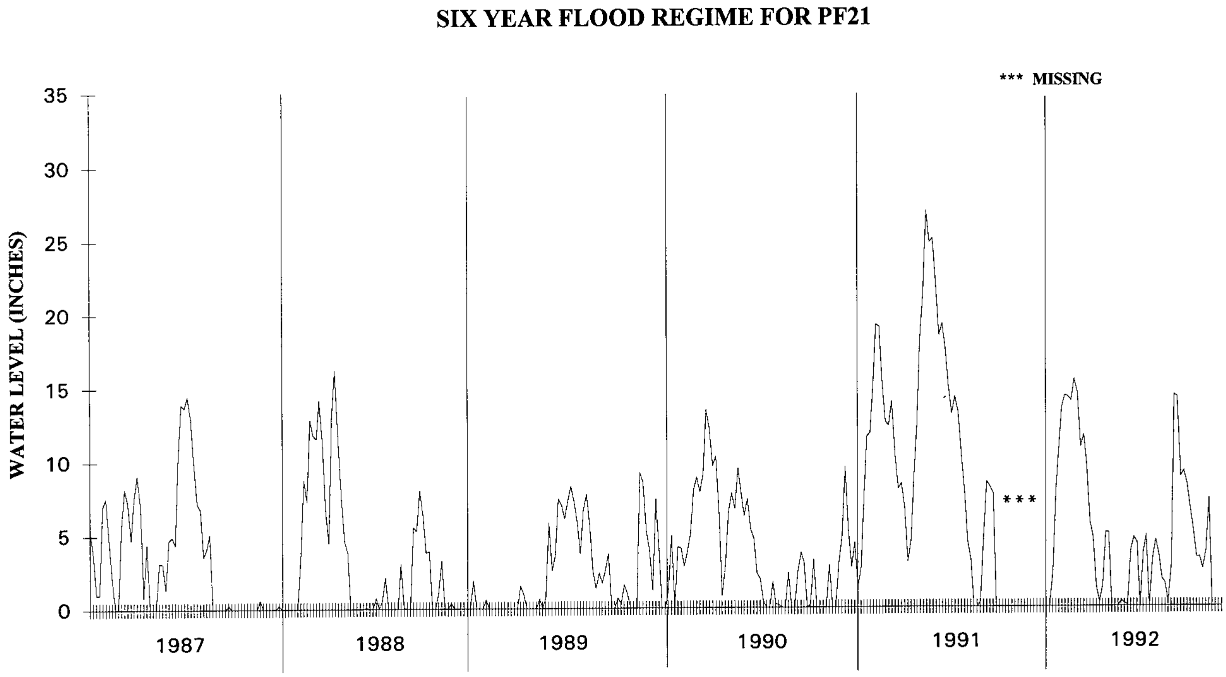


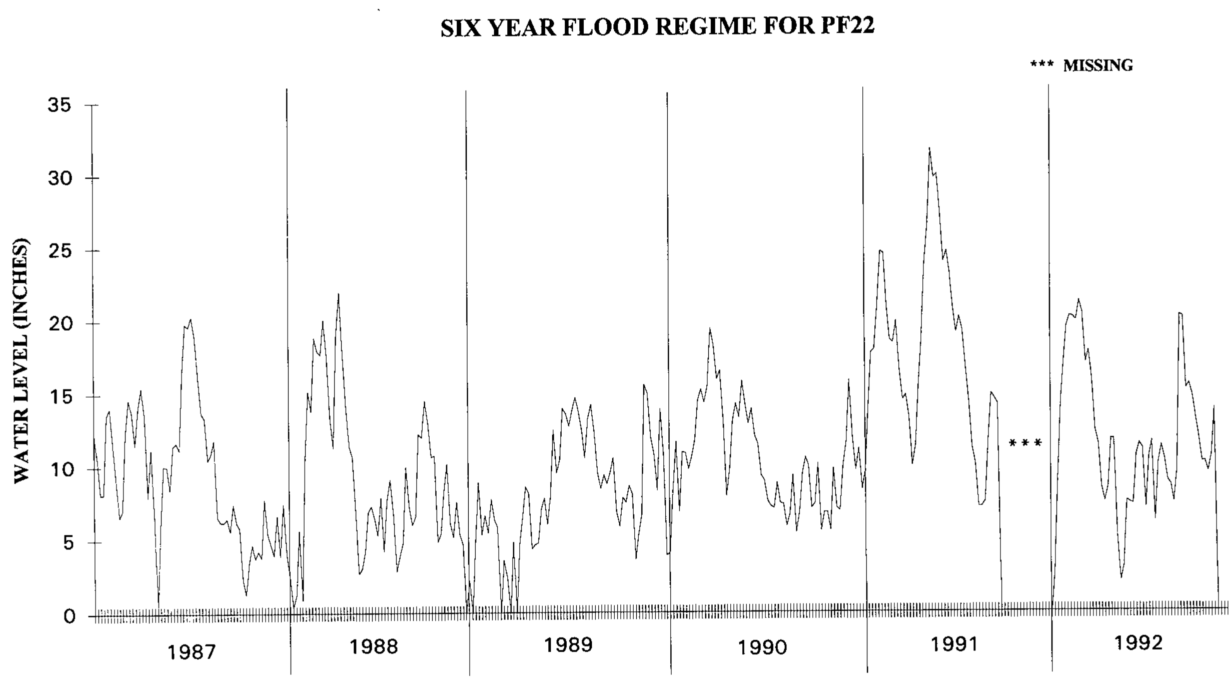
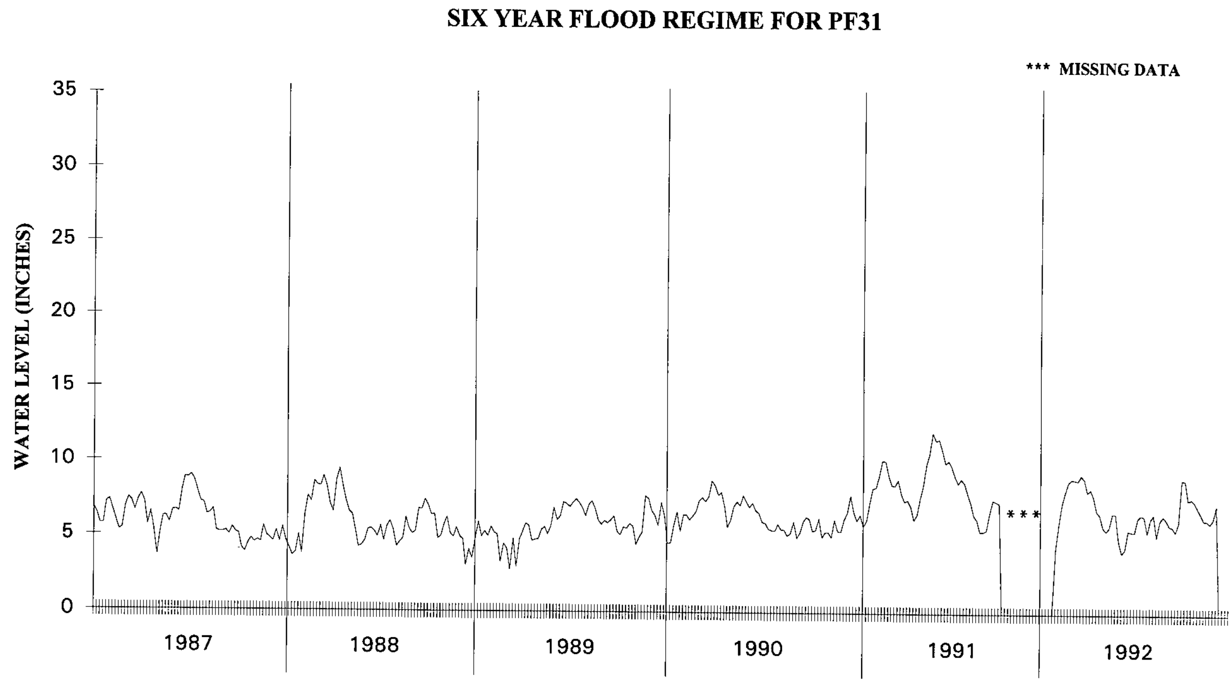


Fig. 9. *Continued.*



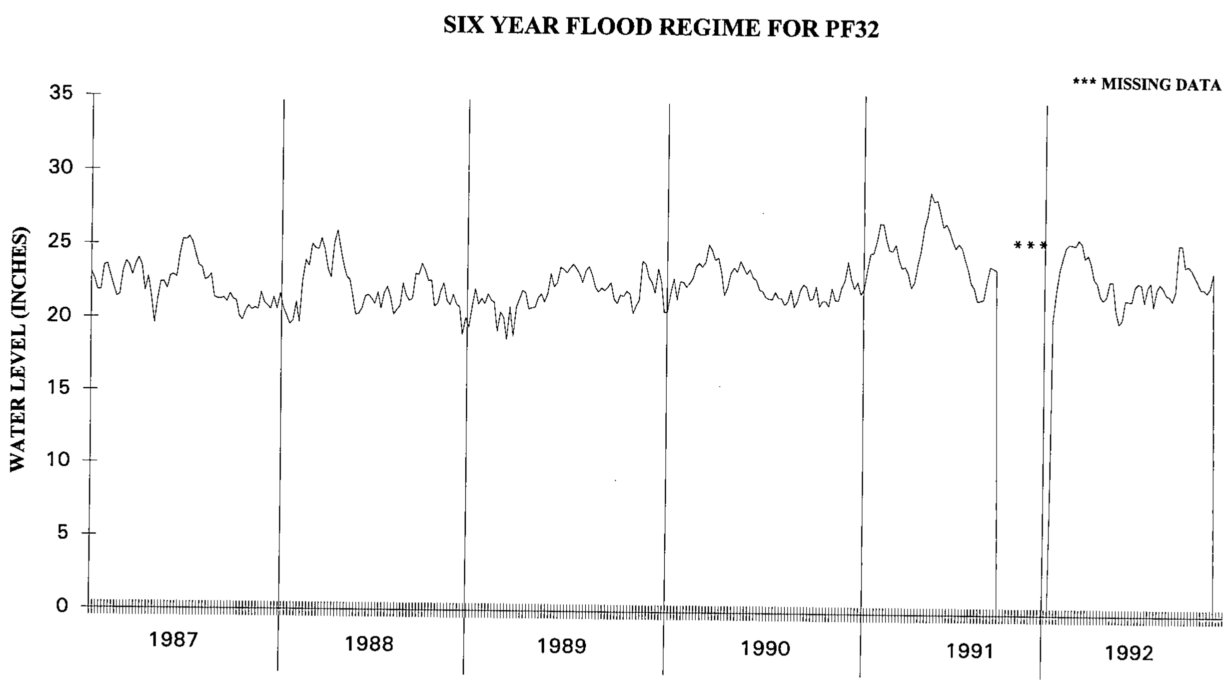


Fig. 9. *Continued.*

Table 2. Regression equations utilized to create historical water levels at Bayou Chevreuil, Louisiana. Equation used was y = a + bx, where y = ____, x = ___, and a and b are regression constant and parametric.

Plot number	Linear regression model[a] [y=a+bx]	Coefficient of determination (r^2)
Seasonally flooded		
1-1	-16.065 + 0.875G[b]	0.98
1-2	-10.676 + 0.868G	0.97
2-1	-13.479 + 0.899G	0.98
2-2	-16.840 + 0.786G	0.98
3-1	-12.017 + 0.694G	0.93
3-2	-10.737 + 0.728G	0.91
Permanently flooded		
1-1	-5.693 +0.753G	0.96
1-2	-5.814 + 0.739G	0.96
2-1	-15.178 + 0.798G	0.97
2-2	-6.593 + 0.724G	0.94
3-1	+1.741 + 0.196G	0.44
3-2	+17.503 + 0.215G	0.42

[a]Depth in inches of water.
[b]G = U.S. Army Corps of Engineers gauge reading in inches.

Importantly, the effects of leafroller defoliation in the Bayou Chevreuil area also differed among hydrologic regimes. The defoliation ratings for 1992 and 1993, and a combined rating for 1992–93 (Fig. 11), indicate higher herbivory levels in seasonally flooded and permanently flooded transects than in nonflooded areas. It can be assumed that photosynthetic losses as a result of increased herbivory by leafrollers acted in concert with flooding duration to reduce radial and volumetric growth of baldcypress in permanently flooded areas.

It should be noted that, though there appears to be minor differences in ages of trees among flooding regimes, all stands contained a similar assemblage of tree diameters and heights. Thus, we are assuming that leaf surface area, etc., are similar enough to make direct comparisons (see Meeker 1992).

There appeared to be little, if any, overall difference in refoliation amounts or intervals with respect to tree size or hydrologic regime. Because there is less volume of foliage on small trees and leafroller populations tend to congregate on smaller trees or the lower branches of larger trees, these areas are

Table 3. Mean tree parameters for baldcypress growing under three hydrologic regimes at Bayou Chevreuil, Louisiana.

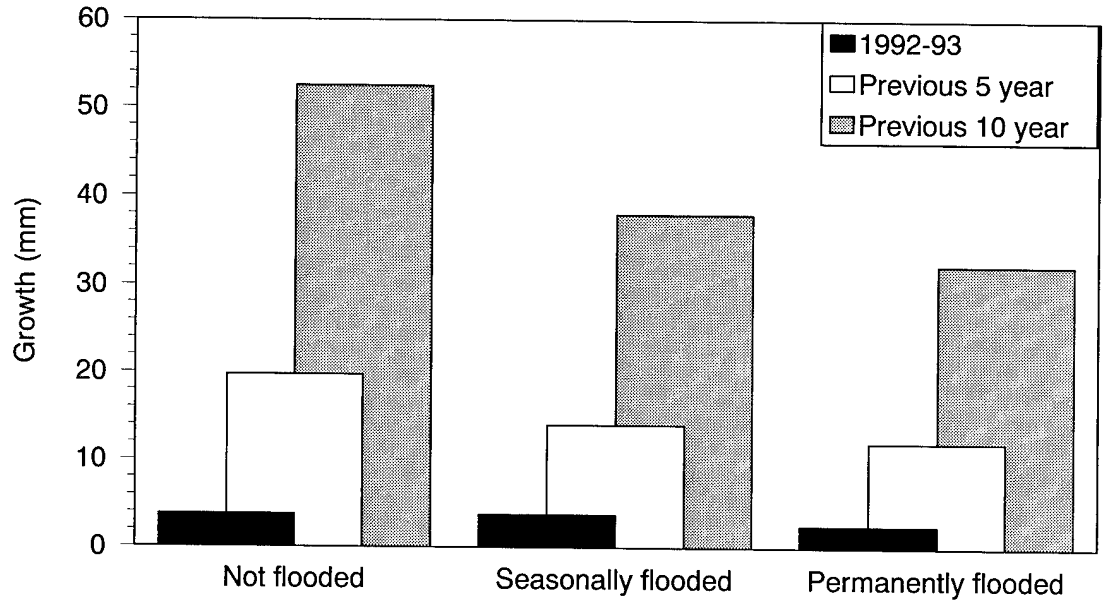
Treatment[a]	Sample size	Diameter[b] (cm)	Age (Years)	1-year growth[c] (mm)	5-year growth[d] (mm)	10-year growth[d] (mm)
Nonflooded	30	38.9	67.8	3.4	19.6	52.4
Seasonally flooded	30	37.8	67.5	3.3	13.9	37.8
Permanently flooded	30	31.8	56.3	2.2	11.6	32.1

[a]Means of three replicates.
[b]Means of two measurements taken at 0.5 m above buttress.
[c]Means of two measurements taken with a Karlberg Microdendrometer.
[d]Means of two cores taken at 0.5 m above trunk buttress.

Table 4. Radial growth of baldcypress (mm) under three hydrologic regimes at Bayou Chevreuil, Louisiana.

	Differences	
Comparisons	5 - Year Growth	10 - Year Growth
Permanently flooded vs. nonflooded	-22.1[a]	-54.0[a]
Seasonally flooded vs. nonflooded	-16.4[b]	-40.1[b]
Seasonally flooded vs. permanently flooded	5.7[b]	13.9[b]

[a]Growth differences significant at $P < 0.05$, Scheffe Post Hoc Test (three replicates combined).
[b]Growth differences not significant at $P < 0.05$, Scheffe Post Hoc Test (three replicates combined).



[a] Measured by Karlberg microdendrometer.
[b] Measured from increment cores.

Fig. 10. Radial growth (mm) of baldcypress for three hydrologic regimes, Bayou Chevreuil, Louisiana.

defoliated first and more severely. The time interval to formation of new buds and subsequently to refoliation did not differ appreciably in weekly evaluations. There was significant tree-to-tree variation in the calendar date of both defoliation and subsequent refoliation. However, when the interaction of habitats and different levels of flooding was evaluated, there were no apparent habitat-specific differences.

Table 5. Basal area growth of baldcypress under three hydrologic regimes at Bayou Chevreuil, Louisiana, 1992-93.

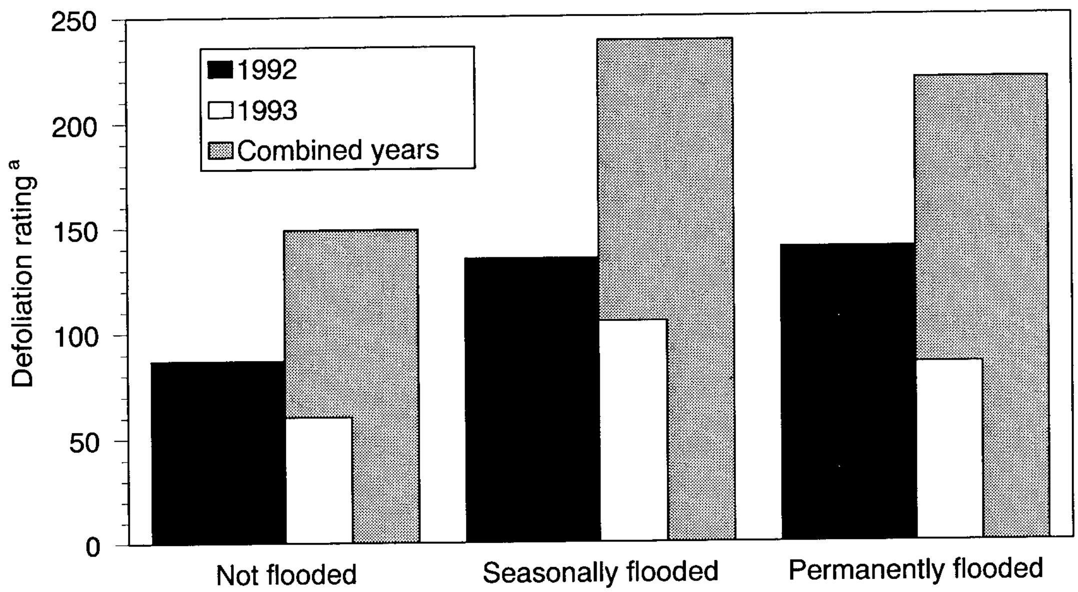
Treatment	Basal area growth (mm²)	Number of trees
Nonflooded	3217	30
Permanently flooded	1092	30
Seasonally flooded	2340	30

Comparisons	Difference (mm²)	Probability[a]
Permanently flooded vs. nonflooded	-2125	0.00
Seasonally flooded vs. nonflooded	-877	0.22
Seasonally flooded vs. permanently flooded	+1248	0.05

[a] Scheffe Post Hoc Tests of ANOVA ($P < .0001$).

Conclusions

The combination of defoliation by the fruittree leafroller and flooding duration has caused significant loss of growth and vigor of baldcypress in forested wetlands of Louisiana. Reduced radial and volumetric growth were most obvious in permanently flooded areas when compared to nearby nonflooded regimes. Of particular ecological concern is the combined effect of insect herbivory and flooding on the health of understory saplings. Often the only woody plants in open patches of stands, the saplings displayed both crown dieback and death as a result of these combined stresses. With inadequate regeneration, larger open patches may occur, affecting the future of these ecologically and economically important bottomland forests. Long-term studies are needed to quantify losses and determine specific causal mechanisms for resource depletion of these forested wetlands.



[a] Rating is the sum of individual tree defoliation classes (1-5; see page 8) multiplied by the frequency of that class for each treatment (30 trees per treatment).

Fig. 11. Baldcypress defoliation rating by fruittree leafroller larvae for three hydrologic regimes, Bayou Chevreuil, Louisiana.

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Appendixes

Appendix A

Stand and growth parameters by treatment for baldcypress, Bayou Chevreuil, Louisiana.

Source	df	Sums of squares	Mean square	F-ratio	Probability
Analysis of variance for growth (1992-93)					
Constant	1	783.6970	783.6970	118.8300	≤0.001
Treatment	2	26.6385	13.3193	2.0195	0.2135
Replicate	6	39.5720	6.5953	1.2458	0.2920
Error	81	428.8340	5.2943		
Total	89	495.0450			
Analysis of variance for age					
Constant	1	333572.0000	333572.0000	629.3700	≤0.001
Treatment	2	2342.0500	1171.0200	2.2095	0.1910
Replicate	6	3180.0400	530.0070	1.7474	0.1222
Error	73	22141.2000	303.3040		
Total	81	27699.0000			
Analysis of variance for DBH					
Constant	1	17903.7000	17903.7000	913.9200	≤0.0001
Treatment	2	140.0840	70.0421	3.5754	0.0950
Replicate	6	117.5410	19.5901	1.6185	0.1530
Error	79	956.2040	12.1038		
Total	87	1207.5200			

Appendix B

Source	df	Sums of squares	Mean square	F-ratio	Probability
Analysis of variance for 5-year growth					
Constant	1	116308.0000	116308.0000	186.1800	≤0.0001
Treatment	2	7025.0300	3512.5200	5.6227	0.0421
Replicate	6	3748.2000	624.6990	2.5597	0.0262
Error	74	18060.0000	244.0540		
Total	82	27696.8000			

Comparison	Difference	Standard error	Probability
Scheffe Post Hoc tests			
PF-NF	-222.6088	6.8090	0.0480
SF-NF	-16.3532	6.8090	0.1325
SF-PF	5.7156	6.7170	0.7105

Appendix C

Source	df	Sums of squares	Mean square	F-ratio	Probability
Analysis of variance for 10-year growth					
Constant	1	856755.0000	856755.0000	313.4000	≤0.0001
Treatment	2	42124.7000	21062.4000	7.7045	0.0220
Replicate	6	16402.7000	2733.7800	1.9776	0.0796
Error	74	102297.0000	1382.3900		
Total	82	156321.0000			

Comparison	Difference	Standard error	Probability
Scheffe Post Hoc tests			
PF-NF	-54.0152	14.2400	0.0255
SF-NF	-40.1148	14.2400	0.0799
SF-PF	13.9003	14.0500	0.6355

Appendix D

Source	df	Sums of squares	Mean square	F-ratio	Probability
Analysis of variance for volume growth					
Constant	1	442254054			
Group	2	65812611	442254054	116.5600	≤0.0001
Error	85	322509689	32906305	8.6727	0.0004
Total	87	388322300	3794232		

Level of group	Expected cell mean	Cell count
Expected cell means of data on groups		
VolGrwNF	3217	30
VolGrwPF	1092	28
VolGrwSF	2340	30

Comparison	Difference	Standard error	Probability
Scheffe Post Hoc tests			
VolGrwPF-VolGrwNF	-2124.5800	511.8000	0.0004
VolGrwSF-VolGrwNF	-876.5290	502.9000	0.2249
VolGrwSF-VolGrwPF	1248.0500	511.8000	0.0565

Appendix E

Source	df	Sums of squares	Mean square	F-ratio	Probability
Analysis of variance for 1992 defoliation					
Constant	1	1237.5000	1237.5000	420.7900	$\leq$0.0001
Treatment	2	1.6009	0.8004	0.2722	0.7706
Replicate	6	17.6452	2.9409	2.2001	0.0515
Error	79	105.6000	1.3367		
Total	87	124.5000			

Appendix F

Source	df	Sums of squares	Mean square	F-ratio	Probability
Analysis of variance for 1993 defoliation					
Constant	1	532.9000	532.9000	210.3600	$\leq$0.0001
Treatment	2	4.2000	2.1000	0.8290	0.4810
Replicate	6	15.2000	2.5333	2.3134	0.0411
Error	81	88.7000	1.0951		
Total	89	108.1000			

Appendix G

Correlation matrix, by treatment, for defoliation and growth parameters of baldcypress. Bayou Chevreuil, Louisiana.[1]

Seasonally flooded	Volume growth	Total defoliation	'92 defoliation	'93 defoliation	5-year growth	10-year growth
Total defol[2]	NS	•	•	•	•	•
'92 defol	NS	+	•	•	•	•
'93 defol	-	+	+	•	•	•
5-yr growth	NS	NS	NS	NS	•	•
10-yr growth	NS	NS	NS	NS	+	•
Mean defol	NS	+	+	+	NS	NS

Permanently flooded	Volume growth	Total defoliation	'92 defoliation	'93 defoliation	5-year growth	10-year growth
Total defol	NS	•	•	•	•	•
'92 defol	NS	+	•	•	•	•
'93 defol	NS	+	NS	•	•	•
5-yr growth	NS	-	NS	-	•	•
10-yr growth	NS	NS	NS	NS	+	•
Mean defol	NS	+	+	+	-	NS

Not flooded	Volume growth	Total defoliation	'92 defoliation	'93 defoliation	5-year growth	10-year growth
Total defol	NS	•	•	•	•	•
'92 defol	NS	+	•	•	•	•
'93 defol	NS	+	+	•	•	•
5-yr growth	+	NS	NS	NS	•	•
10-yr growth	+	NS	NS	NS	+	•
Mean defol	NS	+	+	+	NS	NS

[1] + or - indicate significant positive or negative correlations at P=0.05; NS = not siginificant at P=0.05; • = duplicate comparison.

[2] Defol is an abbreviation for defoliation.

Appendix H

Correlation matrix, for defoliation and growth parameters of baldcypress, combined treatments, Bayou Chevreuil, Louisiana.[1]

Combined treatments	'92 defoliation	'93 defoliation	5-year growth	10-year growth
93 defol[2]	**+**	•	•	•
5-yr growth	**NS**	**NS**	•	•
10-yr growth	**NS**	**NS**	**+**	•
1-yr growth	**-**	**-**	**NS**	**+**

[1] + or - indicate significant positive or negative correlations at P=0.05; NS = not siginificant at P=0.05; • = duplicate comparison.

[2] Defol is an abbreviation for defoliation.

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13. ABSTRACT (Maximum 200 words)
This project was undertaken to delineate the extent of defoliation of baldcypress and to compare defoliation and refoliation rates under different flooding regimes in naturally occurring field situations. Three hydrologic or flooding regimes are compared: nonflooded, seasonally flooded, and permanently flooded. Baldcypress radial growth, short-term basal area increments, dieback or tree canopies, and historical growth and flooding levels are evaluated. Fruittree leafroller defoliation of baldcypress was compared in 1992 to 1993 showing sufficient damage each year so that significant loss of radial and basal area growth resulted when combined with the effects of increased flooding levels and duration. Reduced growth after increased insect defoliation was compared in permanently flooded areas with nonflooded regimes. Combined effect of insect defoliation and flooding on the health and survival of understory baldcypress saplings shows both canopy dieback and death. The fruittree leafroller appears to be important in furthering the rapid decline of baldcypress in the ecologically and biologically important wetlands.

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As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This responsibility includes fostering the sound use of our lands and water resources; protecting our fish, wildlife, and biological diversity; preserving the environmental and cultural values of our national parks and historical places; and providing for the enjoyment of life through outdoor recreation. The Department assesses our energy and mineral resources and works to ensure that their development is in the best interests of all our people by encouraging stewardship and citizen participation in their care. The Department also has a major responsibility for American Indian reservation communities.

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